THE POPULATION DYNAMICS OF LAKE TROUT (*SALVELINUS NAMAYCUSH*) IN LAKE MANITOU, IN RELATION TO THE PLANTING AND SPAWN-TAKING OPERATION

B.A. Henderson

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R.R.# 1 Tehkummah – Ontario
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ABSTRACT

Henderson, B.A. 1982. The Population Dynamics of Lake Trout (*Salvelinus namaycush*) in Lake Manitou, in Relation to the Planting and Spawn-Taking Operation. Ont. Fish. Tech. Rep. Ser. No. 5: iv + 14p.

Lake Manitou has been used increasingly for angling and recreation, and as a source of lake trout (*Salvelinus namaycush*) eggs. An increasing number of trout have been introduced to compensate for this increased use of trout. The ratio of native to planted fish has fluctuated since 1963, but in recent years has fallen to a sustained low level, indicating poor recruitment. The purpose of the study was to determine why recruitment levels have fluctuated and fallen to a sustained low value. Lake trout caught in trap nets set on spawning shoals during the spawn-taking operation provided nearly all the information on population size, age composition, year-class strength, and mortality rates. An annual winter creel census gave an estimate of angling mortality.

Population sizes of planted trout have increased consistently, but the number of native trout has fluctuated over the years and is now low. Recruitment to age 7 from the first two plants was 26%, but subsequently fell to approximately 5%. Natural recruitment reached two peaks in 1965 and 1973, but since then has fallen to a sustained low level, corresponding to a decline in year-class strength. A simulation model of population dynamics showed that the first two peaks of natural recruitment were a function of reproduction of the planted stock. Although the decline in recruitment, in recent years, was a function of change in age composition and fecundity of the spawning population, the sustained low level of recruitment was not anticipated by the model. These variations in recruitment were not a function of either mortality rates or spawn-taking. Mortality at the egg or larval stage may be the main cause of variations in recruitment.

Keywords: lake trout, population dynamics, spawn-taking, recruitment, planted fish, simulation model

THE POPULATION DYNAMICS OF LAKE TROUT *(Salvelinus namaycush)* IN LAKE MANITOU, IN RELATION TO THE PLANTING AND SPAWN-TAKING OPERATION

INTRODUCTION

The splake *(Salvelinus namaycush X S. fontinalis)* and backcross programme for the rehabilitation of the trout populations in Lake Huron has been dependent upon Lake Manitou as a source of lake trout eggs. Since 1959, approximately one million eggs have been taken annually from spawning females. To compensate for this loss, lake trout yearlings have been planted annually in Lake Manitou, since 1959, using mostly native stocks. Splake and backcross developed from Lake Manitou's trout subsequently have been planted in southern Georgian Bay, near Heywood and Burnt Islands, South Bay, and off the southern end of Manitoulin Island. The programme for the rehabilitation of trout in Lake Huron will be dependent upon Lake Manitou's trout for many years.

Apart from Manitou's importance to the rehabilitation programme, the lake is being used increasingly for recreation; more boats and anglers are using the lake each year and there is pressure to develop more of the shoreline for cottages. If this trend continues, the lake trout population may be in jeopardy. The present study was undertaken because it appeared that there were fewer naturally-recruited trout in both the angler's catch and trap nets than in previous years.

Little detailed information about the population dynamics of lake trout in Lake Manitou has been collected, but winter creel census data, collected since 1962, and records of trap-netting on spawning shoals since 1958 provided some information about numbers, sex ratio, age-class structure of spawning and harvested fish, growth and survival. This study was designed to answer the question: *Does the expected recruitment to the spawning population differ significantly from the observed?* Observed values were obtained from catch statistics, and expected values from a computer simulation model based on the known parameters of the trout population. The simulation model was used to assess the effects of spawn-taking, angling, and planting size on variation in the abundance of trout. The first part of the paper describes the population dynamics gleaned from the creel census and trap-netting data; the second part describes the simulation model, its results and comparisons with available information.

METHODS

TRAP-NETTING ON SPAWNING SHOALS

Since 1959, trout have been caught in trap nets on seven shoals, but annually only from two shoals, Maple and Watson's (Fig.1). The analysis of data in this study was confined to trout caught on the latter two shoals. The nets at these two locations (32 mm stretched crib mesh) were set at a depth of 5.5 m in early October and removed when sufficient numbers of eggs were obtained. The number of native and clipped or planted trout, sex ratio, number of females spawned, and egg volume were recorded for each net, each year.

Analytical Techniques

Age Composition and Catch per Unit of Effort. The CPUE of native and planted trout was found by dividing the number caught (Cij) by the number of days that the net was set (Eij). Planted trout were recaptured more frequently within the year than native trout, so the catch was corrected using the following equation:

$$MRj = \frac{\sum_{k=1}^{1} Rkj}{\frac{n}{\sum_{k=1} Rkj}} \qquad \text{Eq. (1)}$$

where j = planted or native trout

k = frequency of recapture in the trap net in the same year.

These data were obtained from individually marked trout caught in 1959 and 1960 (Budd et al 1968); it should be noted that these planted fish were non-native and were hard at this time. Consequently, I may have exaggerated the difference between native and planted stocks. Therefore, the CPUE was found by the equation:

$$CEij = \frac{Cij \times MRj}{Eij} \qquad \text{Eq. (2)}$$

where i = year of capture. The total population estimate was determined from the regression of the population estimate for tagged fish (Budd et al 1968) and the CPUE of tagged fish caught in the Maple trap net as follows:

$$Sij = 76.22\ CEij - 63.02 \qquad \text{Eq. (3)}$$

where Sij = population estimate ($P < 0.01$, $r = 0.93$).

Knowing the age-class structure (fYm) and the population size, one can estimate the number of fish at the peak of the catch curve by the following means:

$$Ym = fYm \times Sij \qquad \text{Eq. (4)}$$

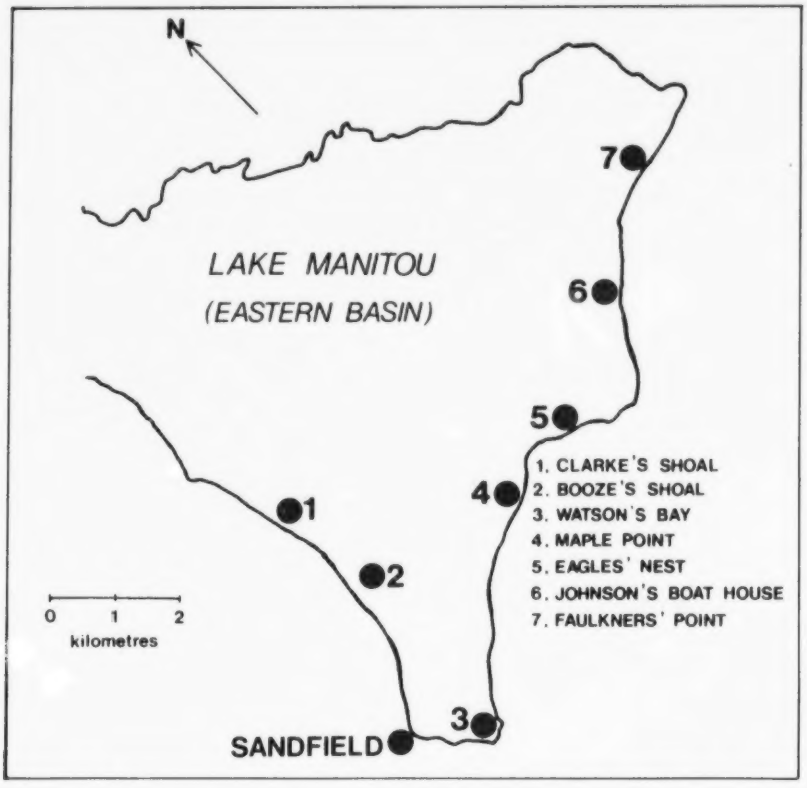

Figure 1. Trap-netting locations in Lake Manitou. One other location, Nigger's Point in the western basin, was fished in 1963.

where m = the age-class at the peak of the catch curve.

The peak of the catch curve was at 6 years of age, but in some years, particularly the early years when there were few older fish, the peak was at 4 or 5. Assuming a stable age-class structure, one could estimate the actual numbers at age 4 or 5 by using the following relationship:

$$\hat{Y}m = \frac{Ym}{rYm} \qquad \text{Eq. (5)}$$

Then, the sizes of the other age-classes could be found by extrapolating to younger:

$$Ym-1,n = \frac{Ym}{1-An}$$

or older:

$$Ym+1,n = Ym(1-An) \qquad \text{Eq. (6)}$$

age-classes, using the mortality rate (An), where n = year-class.

The sum of the contributions from each age-class provided an estimate of the total population size:

$$Pi = \sum_{m=1}^{20} \sum_{n=1}^{1} Ymn \qquad \text{Eq. (7)}$$

where Pi = population size in the i^{th} year.

Effect of Spawning Operation. The proportion of spawners (PSij) artificially spawned was obtained by summing the number of native or planted females spawned (Fij) and dividing by the estimate of the number of spawners (Sij), as follows:

$$PSij = \frac{Fij}{SRi \times Sij} \qquad \text{Eq. (8)}$$

where SRi = sex ratio.

Mortality Rates. The CPUE was determined for each year-class of planted fish caught in the trap nets each year. This CPUE was transformed to natural logarithms and a regression on age gave the survival rate (Sn) by taking the anti-logarithm of the regression coefficient. This estimate of survival rate was determined from the descending right limb of the catch curve. An alternate method was needed to estimate the survival of younger fish. Firstly, the proportion that survived to age 7 provided an estimate of total survival (TSn). Then the annual survival rate was calculated from:

$$e^{(\ln Tsn)/n-1} = S_n \qquad \text{Eq. (9)}$$

for the age 1 to 7. The divisor is n-1 because there are six intervals between age 1 and 7. If one assumed that mortality from 1 to 7 consisted of both fishing and natural mortality, whereas there was little or no fishing mortality later, the difference between the two estimates of instantaneous mortality rates provided an estimate of the fishing mortality from age 1 to 7.

Maturation Schedule. For the years 1959-1962, and 1969 at the Maple net, the CPUE of the age-classes younger than the peak of the catch curve was determined by extrapolation with known survival rate. The percentage of the observed to the expected provided a measure of the percentage maturation, assuming that trout caught in the trap nets were mature. The average percentage for these years was used to obtain the maturation schedule.

CREEL CENSUS

Each winter from 1962 to 1979, with the exceptions of 1969 and 1973, a creel census was taken from January to April. The information collected during the census was used to find the age-class distribution of the harvest, growth, and total harvest.

Total Harvest of Trout

Two methods were used to estimate the total harvest of trout.
Method # 1.
Knowing the number of anglers interviewed over the census period (ACi), the number of census days (Ci), and the catch (Ti), one could calculate the number of anglers per census day (ACi/Ci) and the CPUE (Ti/ACi). Assuming that the creel census could only cover approximately one-half of the anglers in one day, and that there were approximately 75 angler-days from January to mid-April, I estimated the angling pressure (Ii) as:

$$Ii = 75 \times 2 \times \frac{ACi}{Ci} \qquad \text{Eq. (10)}$$

and then the total harvest (Hi) as:

$$Hi = Ii \times \frac{Ti}{ACi} \qquad \text{Eq. (11)}$$

From two years when both a summer and winter creel was done, it was found that the winter harvest was 1.82 times the summer catch, therefore, the total catch for the year was the sum of the winter plus 0.55 (1/1.82) times the winter harvests.
Method # 2.
In some years less information was available so that the total catch in the winter was obtained by:

$$\sum_{z=1}^{3} \frac{Tiz}{Ciz} \times 20 = Hi \qquad \text{Eq. (12)}$$

where z = the number of months fished.

Again, it was assumed that the summer catch was 0.55 times the winter one.

The two estimates of harvests were significantly correlated ($r_s = 0.61$, $P < 0.05$), so an average value was calculated, if possible. The fishing mortality rate (Mi) was obtained by dividing the harvest (Hi) by the size of the harvestable population (catch in fall trap nets used to estimate harvestable population):

$$\frac{Hi}{\sum_{m=1}^{m} HA_m \times Pi} = Mi \qquad \text{Eq. (13)}$$

where HA_m = the proportion of fish harvested at each age,
and Pi = population size in year (i).

Growth Rate

The size (fork length) at age was obtained from the creel in 1966, 1970-71, and 1975-77, by a regression of fork length (cm) on the natural logarithm of the age plus one. The length-weight equation ($W = nL^3$) was derived from the 1977 creel census.

SIMULATION MODEL

The main objective of constructing a simulation model was to compare the observations derived from field studies in Lake Manitou with the expected results obtained from a simulation model, using information about planting schedule, survival rates, maturation, growth, and fecundity, derived for the most part from these studies. The question was: *Is recruitment less than expected?*

Assumptions of Model

Survival Rates. The survival rate of the young fish (1-7) was less than for the older fish, primarily because fishing mortality acts on this group. The survival rates of the eggs and fry were 10 and 5%, respectively.

Growth Rates. The equation for growth in fork length (cm) with age (AJ) was:

$$L_{ij} = G_{ij} \ln (A_j + 1) - C$$

and

$$G_{ij} = 30e^{-aW_{ij}}$$

so that the population size

$$W_{ij} = \sum_{j=1}^{20} P_{ij}$$

depresses the rate (G_{ij}) of growth.

Maturation and Fecundity. Maturation (Fig. 2) and fecundity

$$F_{ij} = (172.74 L_{ij} = 5941.43) \times D_{ij} \times 0.8$$

were both dependent upon size. The realized fecundity was a function of population size

$$D_{ij} = 1.16e^{-aW_{ij}}$$

with an increase in population size causing a decrease in recruitment. The spawn-taking operation was assumed to remove only 10% of the eggs.

RESULTS

PLANTING SCHEDULE AND RECRUITMENT TO SPAWNING POPULATION

The first trout introductions in Lake Manitou were made in 1952. Since 1959, there has been an annual planting, with the size of the plant increasing in recent years (Table 1). The percentage survival to age 7 was high for the first two plants, but has been substantially smaller since then (Table 2). This drop in recruitment may be a function of plant size or increasing population size of the planted stock. Walker (1979) found that a polynomial regression described the relationship between the date of planting and the proportion that survived to age 6. I found no significant regression for either Maple ($Y = 0.0280 + 0.0127X - 0.0004X^2$, $P > 0.05$) or Watson's nets ($Y = 0.0130 + 0.072X - 0.0001X^2$, $P > 0.05$).

MORTALITY RATES

The CPUE of each year-class of planted fish is shown on Table 3. Not all of the year-classes were amenable to this analysis because a few had the same code, and for later ones, there were too few age-classes. The average annual survival rates of 69.9 and 68.1 for Maple and Watson's, respectively, are similar (Table 4); these values are somewhat lower than the estimate of 75% derived by Budd et al (1968) for the 1952 year-class of planted fish.

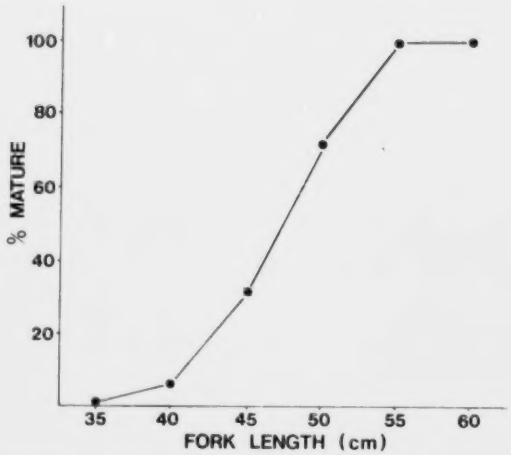

Figure 2. Maturation schedule for Lake Manitou's trout.

The survival rate for the younger fish was usually lower than for the spawning population (Table 2), except for the first two year-classes and 1969. Variation in the survival rate of the younger fish (1-7) was the result of fishing, natural, and planting mortality, whereas variation in the survival rate of the spawning population was mainly caused by natural mortality. This was supported by the observation that the age-class distribution of the harvest is quite distinct from the spawning population (Fig. 3). Therefore,

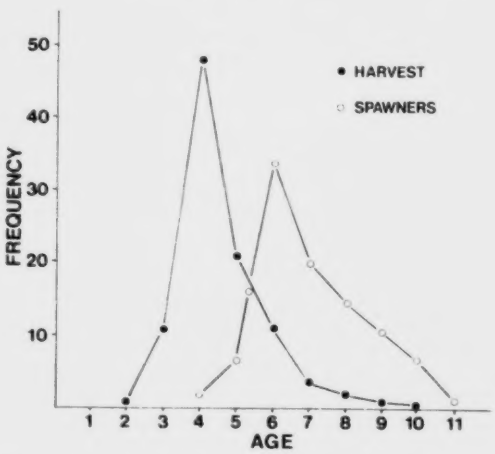

Figure 3. The age-class distribution of the harvested and spawning population.

Table 1. The date of planting, number, length, weight, and clipping code of trout introduced to Lake Manitou.

Year Stocked	Weight (gm)	Fork Length (cm)	Total no. Stocked	Fin Clip	Date Stocked
1977	9.0	9.7	40,000 20,000	R.V. R.V. & A.	Mar. 30, 31 Apr. 25
1976	7.6	9.1	40,000 20,000	R.P. R.P. & A.	Apr. 12, 13 June 3
1975	8.5	9.9	20,000 19,918	A. L.P.	Apr. 7 Oct. 14
1974	6.0	9.4	60,000	L.V.	May 1, 2
1973	8.2	8.4	40,000 20,000	A. L.V. & A.	Mar. 29 Apr. 26
1972	7.5	9.1	50,000	R.V.	Apr. 5
1971	9.0	9.7	29,000	R.P.	Apr. 27, 29
1970	8.3	9.4	42,000	L.P.	Apr. 10, 14
1969	6.4	8.6	20,040 21,960	L.V.	Apr. 18, 22
1968	5.4	8.1	65,000	A.	May 17, 28, 30
1967	5.4	8.1	53,000	R.P.	June 23
1966	4.0	7.4	30,000	R.P. & A.	May 16
1965	5.4	8.1	10,000	R.P. & L.V.	May 31
1964	5.4	8.1	26,900	L.P. & A.	June 8
1963	5.0	8.1	29,980	A.	May 29
1962	9.0	9.7	14,950 13,975	L.V. & A. L.V. & A.	May 10 Oct.22
1961	5.2	8.1	10,640	L.P. & R.V.	May 31
1960	3.3	7.1	14,000	R.V.	May 7, 10
1959	4.3	7.6	10,000	L.V.	May 12
1958	3.0	6.4	29,000	A.	May
1952	9.2	9.4	10,000	A.	Nov.

the difference between the instantaneous rates for the young (1-7) and old (7-12) fish could be used to estimate fishing mortality (17.2 ± 3.19%) (Table 4). The estimate of average fishing mortality determined from the creel census was 18.7 ± 4.39 % (Table 4).

GROWTH RATE

The growth at age ($L = 30.04 \ln (A + 1) - 8.86$) was intermediate between the growth rate of trout in Lake Louisa ($L = 24.31 \ln (A + 1) + 10.87$), a planktivorous population, and in Redrock Lake

Table 2. The number of planted fish at age 1 and their percentage survival to age 7.

Year	MAPLE		WATSON'S		Plant size (x1000)	Average %	Annual percent survival to age 7
	CPUE 7	%[a]	CPUE 7	%[a]			
1952	18.73	31	13.30	22	10	26.5	80
1959	9.03	15	25.03	41	10	26.0	80
1960	6.49	8	3.78	4	14	6.0	63
1961	1.73	3	2.32	4	10.6	3.5	57
1962	28.22	16	15.64	9	29	12.5	71
1963							
1964	12.55	8	3.22	2	27	5.0	61
1965	2.94	5	0.79	1	10	3.0	56
1966	7.10	4	9.12	5	30	4.5	60
1967	10.80	3	29.00	9	53	6.0	63
1968							
1969	47.94	19	20.91	8	42	13.5	72
1970	4.62	2	1.23	0.4	42	1.2	48
1971	9.87	6	9.21	5	29	5.5	62
1972	26.20	9	13.07	4	50	6.5	63
						$\bar{x}$%s	61.5

[a] Percentage that survived to age 7

$(L = 42.23 \ln (A + 1) - 38.98)$, where the trout eat perch (Martin 1952). The length-weight relationship ($W = 4.63 \times 10^{-5} L^{2.7804}$) indicated that the trout were more slender than trout from many other areas (Carlander 1969).

POPULATION SIZE

The population size of planted trout was determined by applying a 61.5% survival rate to the year-class until the sixth age-class, then 69% for the remaining age-classes (Table 5). The total population size increased from 1959 to the present. The spawning population (ages 6-10) first appeared in 1957 with a major increase in size in 1963. Subsequently, the spawning population size decreased, then increased from 1970 (Fig. 4). The contribution of each class to each year can be assessed from Table 5. There was a significant correlation ($P < 0.05$) between the estimate of the spawning population size, derived from Equation (3), and the size determined from the matrix (Table 5). This finding would seem to support the estimate of the total population size. Nevertheless, the estimate from the matrix (Table 5) was larger than that found from Equation (3) (Equation estimate = 0.66 matrix estimate + 4.2). The matrix method may be more sensitive to variations in year-class strength than the equation method and, therefore, may be more accurate.

The size of the native population, or more appropriately the unmarked trout, was again found by the matrix method, but with different assumptions. The age-class structure of the spawning population was applied to the estimate of its size and from this, the size of the sixth age-class determined. Then, the other age-classes in each year-class were found by extrapolation, using two different survival rates: 61.5% from 1-6 and 69% from 7-15 (Table 6). By this method, one could determine with some confidence the variation

Table 3. The CPUE of trout caught in the trap nets on Watson's and Maple spawning shoal.

Date	Native	A	RV	LV	RP/LV	LP/RV	Tagged	LV/A	RP/A	LP/A	RV/A	RP	LP	Effort (days set)
MAPLE SHOAL:														
1959	22.8	13.2	0.0	0.6	0.0	0.0	8.9	0.0	0.0	0.0	0.0	0.0	0.0	16
1960	17.6	13.8	0.0	0.5	0.0	0.0	9.0	0.0	0.0	0.0	0.0	0.0	0.0	18
1961	15.3	19.3	0.0	0.5	0.0	0.0	5.2	0.0	0.0	0.0	0.0	0.0	0.0	20
1962	11.0	23.0	0.0	1.9	0.0	0.0	4.0	0.0	0.0	0.0	0.0	0.0	0.0	20
1963	13.9	27.7	5.4	21.8	0.0	0.0	1.2	0.0	0.0	0.0	0.0	0.0	0.0	18
1964	27.6	11.3	13.3	25.9	0.0	0.0	1.3	0.0	0.0	0.0	0.0	0.0	0.0	8
1965	22.1	5.7	9.1	8.8	0.0	6.2	0.8	0.0	0.0	0.0	0.0	0.0	0.0	13
1966	31.9	7.1	6.5	9.1	0.0	13.4	0.5	11.9	0.0	0.1	0.0	0.0	0.0	16
1967	5.1	7.1	0.9	1.8	0.0	1.7	0.1	6.9	0.0	0.7	0.0	0.0	0.0	15
1968	10.6	46.0	5.1	3.9	0.0	6.9	0.0	28.3	0.0	3.8	0.0	0.0	0.0	9
1969	4.6	14.9	2.3	2.8	0.6	1.3	0.0	4.4	0.0	1.3	0.0	0.0	0.0	14
1970	9.9	35.5	1.1	1.1	10.9	2.3	0.0	9.2	15.1	12.5	0.7	0.3	0.0	15
1971	22.9	8.3	0.1	0.3	2.9	0.8	0.0	3.1	12.2	2.0	0.3	1.9	0.0	29
1972	37.6	10.6	0.5	0.9	1.8	0.3	0.0	2.3	7.1	1.1	0.2	10.1	0.0	13
1973	60.0	17.6	0.6	5.2	1.6	0.0	0.0	0.8	4.4	0.6	0.0	10.8	0.0	5
1974	53.4	69.8	2.1	47.8	0.4	6.5	0.0	2.4	5.6	0.3	0.1	19.6	0.0	8
1975	54.2	38.9	2.1	39.3	0.8	0.3	0.0	2.2	4.4	1.4	0.1	39.7	13.3	19
1976	15.8	13.8	13.8	12.1	0.2	0.1	0.0	3.8	1.8	0.0	0.1	35.3	4.6	13
1977	6.9	30.0	10.4	6.4	0.1	0.0	0.0	21.6	0.4	0.0	0.2	9.9	1.7	10
1978	26.1	73.3	26.2	16.4	0.3	0.4	0.0	56.9	1.7	0.3	0.3	19.6	4.2	15
1979	13.9	36.3	10.3	9.9	0.3	0.0	0.0	33.0	1.0	0.3	0.0	9.6	2.8	8
WATSON'S SHOAL:														
1959	8.3	11.8	0.0	0.2	0.0	0.0	7.0	0.0	0.0	0.0	0.0	0.0	0.0	17
1960	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0
1961	6.9	9.6	0.0	0.3	0.0	0.0	3.6	0.0	0.0	0.0	0.0	0.0	0.0	18
1962	7.2	11.4	0.0	1.2	0.0	0.0	3.6	0.0	0.0	0.0	0.0	0.0	0.0	19
1963	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0
1964	19.4	6.4	9.8	21.3	0.0	0.0	1.4	0.0	0.0	0.0	0.0	0.0	0.0	8
1965	62.3	18.5	25.0	24.9	0.0	7.5	1.2	0.0	0.0	0.0	0.0	0.0	0.0	11
1966	15.5	2.1	3.8	5.5	0.0	5.7	0.2	6.5	0.0	0.2	0.0	0.0	0.0	17
1967	11.9	15.1	2.1	2.5	0.0	2.3	0.2	15.0	0.0	0.5	0.0	0.0	0.0	16

Table 3 continued on page 8.

Table 3. The CPUE of trout caught in the trap nets on Watson's and Maple spawning shoal (continued).

Date	Native	A	RV	LV	RP/LV	LP/RV	Tagged	LV/A	RP/A	LP/A	RV/A	RP	LP	Effort (days set)
WATSON'S SHOAL (continued):														
1968	2.8	20.8	2.5	1.6	0.0	2.4	0.0	15.6	0.0	1.2	0.0	0.0	0.0	10
1969	5.0	21.6	2.6	2.4	0.1	1.8	0.0	7.5	0.0	1.1	0.1	0.0	0.0	14
1970	7.9	8.1	0.2	0.2	2.9	0.3	0.0	3.4	5.1	3.2	0.1	0.2	0.0	7
1971	6.0	3.2	0.2	0.3	0.8	0.2	0.7	2.8	3.3	0.0	0.0	0.1	0.0	24
1972	43.5	20.0	1.2	1.5	3.2	0.2	0.1	5.5	9.2	1.5	0.1	9.4	0.0	13
1973	100.2	76.2	1.2	8.2	3.8	0.0	0.0	3.0	6.8	0.6	0.0	29.0	0.0	5
1974	53.4	69.8	2.1	47.8	0.4	6.5	0.0	2.4	5.6	0.3	0.1	19.6	0.0	8
1975	20.6	29.4	1.6	20.9	0.9	0.3	0.0	1.7	3.3	0.4	0.1	17.4	7.5	18
1976	7.5	6.7	5.2	4.2	0.0	0.0	0.0	1.4	1.2	0.1	0.0	9.1	1.2	13
1977	7.6	21.0	13.3	4.2	0.2	0.3	0.0	20.0	0.4	0.1	0.3	9.3	2.1	16
1978	9.4	44.8	13.1	6.6	0.1	0.0	0.0	30.1	0.8	0.3	0.1	8.3	2.1	19
1979	11.8	47.4	9.7	17.2	0.0	0.1	0.0	38.0	2.2	0.2	0.2	10.4	5.8	12

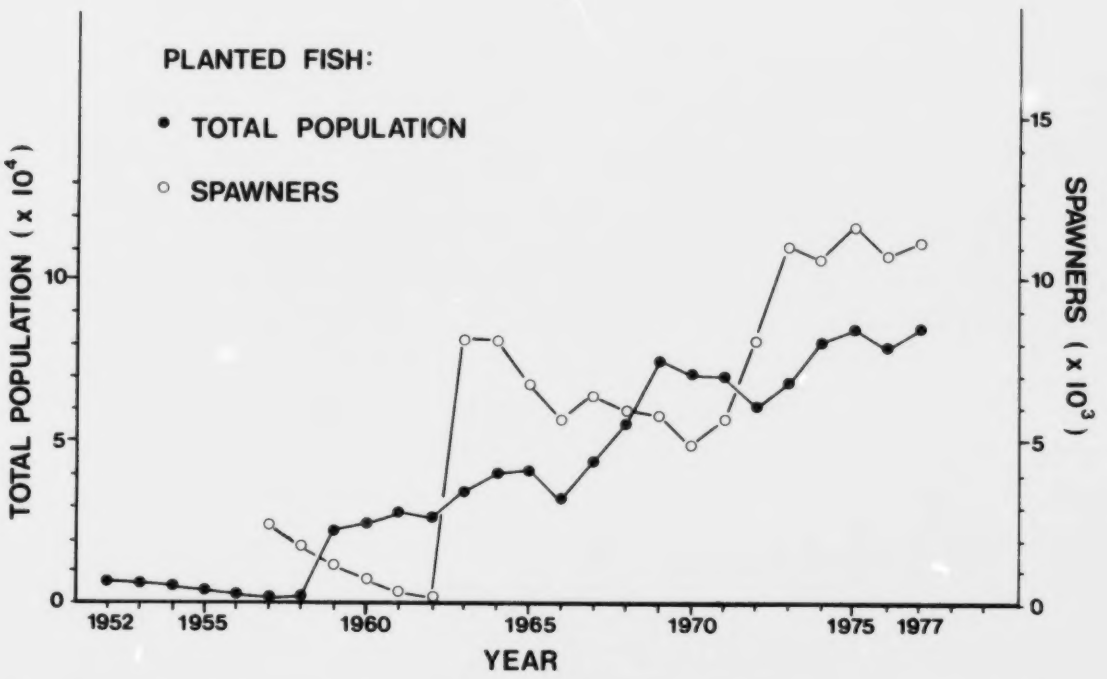

Figure 4. Variation in the numbers of planted fish in both the spawning and total population from 1952 to 1977.

Table 4. The mortality rates for the spawning population caught at Watson's and Maple trap nets (catch curve), and the fishing mortality calculated from the creel census.

Year	MAPLE SHOAL Natural mortality Age 7-12	WATSON'S SHOAL Natural mortality Age 7-12	Fishing mortality Age 2-6
1952	37	26	
1959	36	39	
1960	31	32	
1961	24	25	
1962	29	22	3
1963			7
1964	27	28	6
1965	34	46	29
1966	29	30	19
1967			10
1968			19
1969	27	59	47
1970	28	28	14
1971	29	16	5
1975			16
1976			9
1977			9
1978			15
1979			66
$\bar{x}$	30.1 ± 1.22	31.9 ± 3.63	18.7 ± 4.39

in total population size from 1962 to 1974. From a peak in 1963, the total population size declined until 1966, increased to another peak in 1969, and then declined (Fig. 5). The spawning population reached a peak in 1967, declined to 1970, peaked again in 1974 and then declined. The estimate of the spawning population derived from Equation (3) was correlated ($P < 0.05$) with the matrix method. The native recruitment varied considerably from 1951 to 1973, with peaks in 1961 and 1967 (Fig. 5). The first peak must have been caused entirely by the native spawners, but the second, by contributions of both native and planted spawners. These variations do not appear to be correlated with either the size of the native and spawning population ($P > 0.05$) or the sum of the 1 to 3's in each year ($P > 0.05$). There was no apparent explanation for this variation.

SPAWN-TAKING

From the estimates of the size of the spawning population (Equation (3)), the percentage of the females artificially spawned was determined (Table 7). The percentage varied between 0.04 and 0.23 and the average was 0.11 ± 0.01 ($\bar{x}$ ± S.E.). Variation in the proportion of females artificially spawned was not correlated ($P > 0.05$) with the changes in year-class strength. Although an average of 34.2 ± 3.26% of the spawners were handled in the trap nets each year, there was no

Table 5. The matrix of year-classes and age-classes for planted trout, determined from applying survival rates to the initial plants.

	AGE														
Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1952	10000														
1953		7700													
1954			5929												
1955				4565											
1956					3515										
1957						2706									
1958	29000						1867								
1959	10000	22330						1288							
1960	14000	7700	17194						889						
1961	10690	8610	5929	13239						613					
1962	28925	6543	5292	4565	10194						423				
1963	29980	17835	4024	3256	8515	7849						282			
1964	26900	18450	10968	2474	2002	2706	5416						201		
1965	10000	16605	11346	6745	1522	1231	1867	3737						139	
1966	30000	6150	10212	6978	4148	936	849	1288	2578						95
1967	53000	18450	3782	6280	4291	2551	645	586	889	1779					
1968	65000	32595	11346	2326	3862	2639	1760	445	404	613	1227				
1969	42000	39975	20045	6978	1430	2375	1821	1214	307	279	423	847			
1970	42000	25830	24584	12328	4291	879	1639	1256	838	212	192	292	584		
1971	29000	25830	15885	15119	7581	2639	606	1130	867	578	146	132	201	403	
1972	50000	17835	15885	9769	9298	4662	1821	418	780	598	399	101	91	139	278
1973	60000	30750	10968	9769	6008	5718	3217	1256	288	538	412	275	69	63	95
1974	60000	36900	18911	6795	6008	3695	3945	2219	867	199	371	284	189	48	43
1975	40000	36900	22693	11630	4148	3695	2549	2722	1531	598	137	256	196	131	83
1976	60000	24600	22693	13956	7152	2551	2549	1759	1878	1056	412	94	176	135	90
1977	60000	36900	15129	13956	8583	4398	1760	1759	1213	1296	729	284	65	122	93
1978	60000	36900	22693	9304	8583	5278	3035	1214	1213	837	894	503	196	45	84
1979	60000	36900	22693	13956	5722	5278	3642	2094	838	837	577	617	347	135	31
1980		36900	22693	13956	8583	3519	3642	2513	1445	578	577	398	425	239	93
1981			22693	13956	8583	5278	2429	2513	1734	997	399	398	275	293	165

correlation between the proportion handled and the variation in year-class strength of native fish ($P > 0.05$). Consequently, one could conclude that the spawn-taking operation had little demonstrable effect on reproduction.

SIMULATION MODEL

In the following results, the 'observed data' were obtained from the creel census, spawn-taking operation, and planting records, whereas the simulation data were derived from the model.

There was no statistical difference between the distribution of the numbers of age 1 fish found in the observed and simulated population from 1958 to 1972 (Kolmogorov-Smirnov test, $P > 0.05$; Fig. 6). The ratio of natively recruited trout to planted ones in the spawning population also showed no difference from 1963 to 1974 (Kolmogorov-Smirnov test on Arcsine transformed ratios, $P > 0.05$; Fig. 7). After 1973 the simulated population produced a higher ratio of native to planted spawners than the observed population. The increase in the ratio of native to planted fish in the simulation model was consistent with the increase in year-class strength seen after 1973; one could not assess the year-class strength of the natives after 1972 because the data were not available.

DISCUSSION

This study was initiated because there was some concern about the apparent drop in the recruitment of trout in Lake Manitou. Since these trout provide a substantial proportion of the eggs used for the trout rehabilitation efforts and are important for angling and other recreation, any adverse changes in the success of trout should be rectified. The design of the analysis was chosen, firstly, to assess the dynamics of the population -- as reflected in the creel census, spawn-taking operation and planting efforts -- and secondly, to utilize this information in a simulation model, ultimately to compare the observed with the expected. The data were collected without this intention, and consequently some assumptions had to be made in the analysis, and these are described in the methods. The simulation model is simply an iteration of matrix multi-

Table 6. The matrix of year-classes and age-classes for native trout, determined from applying survival rates to six year old fish.

	AGE														
Year	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
1952															
1953															
1954	5889														
1955	3025	3533													
1956	1991	2115	2120												
1957	1620	1392	1479	1272											
1958	2493	1133	973	1034	763										
1959	4233	1743	792	680	723	458									
1960	7479	2960	1219	554	476	506	320								
1961	4233	5227	2070	852	387	333	354	224							
1962	1606	2960	3655	1447	596	271	233	247	157						
1963	1243	1124	2070	2556	1012	417	189	163	173	69					
1964	873	869	787	1447	1787	708	291	132	114	121	76				
1965	1620	610	608	551	1012	1251	495	204	92	79	85	53			
1966	2619	1133	426	425	385	708	875	346	143	65	55	59	37		
1967	8473	1831	792	298	297	270	495	612	242	100	45	39	41	26	
1968	14333	5925	1280	554	208	208	188	346	429	169	70	31	27	29	18
1969	9471	10023	4143	895	387	146	145	131	242	300	118	49	22	19	20
1970	6727	6623	7009	2897	626	271	102	101	91	169	210	83	34	15	13
1971	2116	4704	4631	4901	2026	438	189	71	71	63	118	147	58	24	10
1972	1369	1480	3289	3239	3427	1417	306	132	50	49	44	83	103	40	16
1973	3241	957	1035	2300	2265	2397	991	214	92	35	34	31	58	72	28
1974	2367	2266	669	723	1608	1584	1677	694	150	65	24	24	22	40	50
1975		1655	1584	468	506	1125	1108	1174	486	105	45	17	17	15	28
1976			1157	1108	327	354	787	776	822	340	73	31	12	11	11
1977				809	775	229	247	551	543	575	238	51	22	8	8
1978					566	542	160	173	385	380	402	166	36	15	5
1979						396	379	112	121	270	266	282	116	25	10
1980							277	265	78	84	189	186	197	81	17

Table 7. The number of both spawning females and females artificially spawned and handled from 1959 to 1979.

Year	Native	Planted	N & P combined	Total females	Females artificially spawned	Females handled	% spawned	% handled
1959	1529	1668	3197	1406	200	692	14	49
1960	1668	1807	3475	2050	162	711	8	35
1961	1112	1459	2571	1002	157	462	16	46
1962	904	1738	2642	1136	109	558	10	49
1963	1390	2502	3892	1401	326	457	23	33
1964	2363	3406	5769	3461	255	1170	7	34
1965	4170	4101	8271	3970	292	1323	7	33
1966	2363	2780	5143	2880	305	910	11	32
1967	9313	2224	11537	6576	238	757	4	12
1968	695	5143	5838	2744	373	555	14	20
1969	487	2432	2919	2218	282	623	13	28
1970	904	4309	5213	2606	240	944	9	36
1971	1460	1668	3128	1282	178	926	14	72
1972	4726	3406	8132	4229	429	1418	10	34
1973	7993	6533	14526	5810	433	477	7	8
1974	5282	11815	17097	12138	543	2135	4	18
1975	3753	8618	12371	7299	504	3404	7	47
1976	1182	4378	5560	3892	640	1745	16	45
1977	765	5769	6534	4965	536	764	11	15
1978	1807	11676	13483	8089	871	3512	11	43
1979	1320	8966	10286	6789	832	1988	12	29
$\bar{x}$ ± S.E.							11 ± 1	34 ± 3

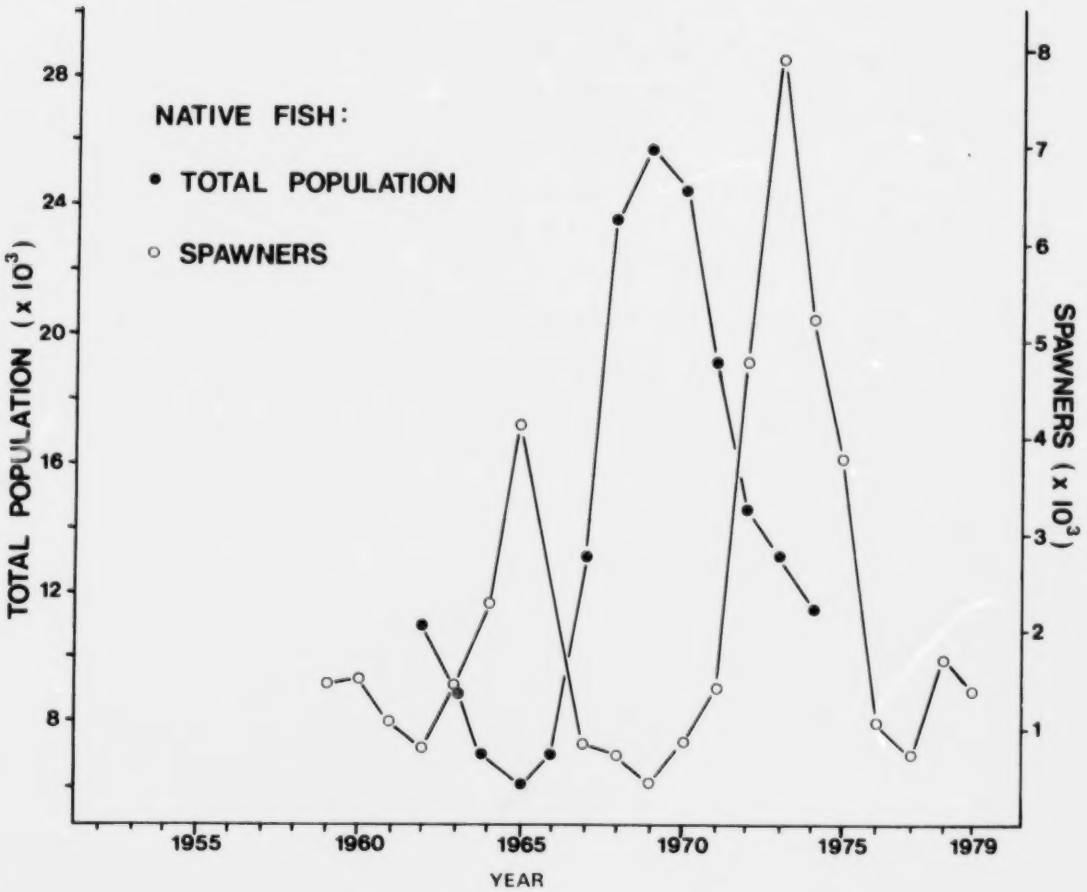

Figure 5. Variation in the numbers of native fish in both the spawning and total population.

plication. Only two internal mechanisms of self-regulation, namely density dependent growth and recruitment, have been included. The following discussion will be divided broadly into two parts: dynamics of the actual and simulated populations.

OBSERVED POPULATION DYNAMICS

In 1952, trout were introduced to Lake Manitou to compensate for what seemed to be a flagging rate of recruitment. Since 1958, plantings have been done annually, with the size of the plant increasing in recent years (Table 1). The first few plants survived well, but survival to age 7 of subsequent introductions was poorer, probably because of the combined effects of increased angling and competition with the extant population growing in number each year (Table 2). There was no indication that success of a planting corresponded to the time of year of the introduction, as shown by Walker (1979). The mortality rates, around 31%, for age-classes from 7 to 12 varied little and fishing mortality for ages 2 to 6 was 19% (Table 4).

The presence of individually marked fish from the 1952 planting (Budd et al 1962) allowed one to estimate the size of the spawning population by comparing the CPUE of tagged trout, their population estimate, and the CPUE of the other plants, distinguished by fin clips (Table 7). From this estimate of the spawning population, one was able to determine the effect of spawn-taking on the reproductive potential (Table 7). Although at least 34% of the spawners were handled, only 11% of the females were artificially spawned for the hatchery programme. The relevance of this information to the population dynamics will be discussed in connection with the simulation model. Knowing the size of the spawning population, one could then estimate the size of the total population by extrapolation on a matrix-format (Tables 5, 6). Having analyzed for these aspects of the population dynamics, one was now able to compare the observations with the theoretical expectations of

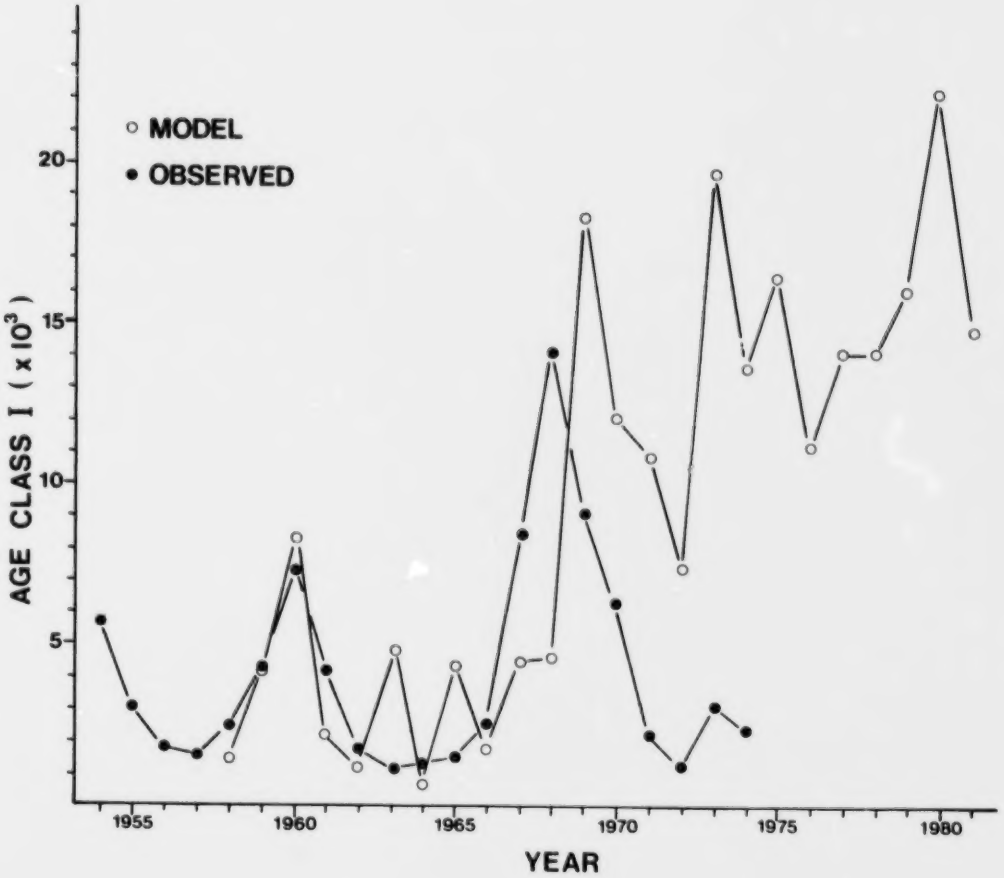

Figure 6. The observed and expected (simulation model) recruitment of age 1 trout to Lake Manitou from 1954 to 1981.

the simulation model.

MODELLED POPULATION DYNAMICS

Two essential comparisons were made: recruitment to age 1 (year-class strength) and the ratio of natives, or naturally recruited trout, to planted trout in the spawning population. From Table 6, the matrix for native trout, the variation in native recruitment could be assessed. The distribution of year-class strength from the simulation model did not differ markedly from the observed recruitment, at least between 1958 and 1972 (Fig. 6). Therefore, one might conclude that the observed dynamics did not deviate significantly from the expected. In addition, no significant difference existed between the ratio of native to planted trout observed from the field studies and the expected ratio from the simulation model, until approximately 1974 (Fig. 7). After this, the observed ratio was less than the expected, indicating some failure in recruitment. In Figure 6, it can be seen that the year-class strength should have improved after 1972, but apparently it did not happen in the natural population. Therefore, one or more factors have acted to depress recruitment or survival during the early 1970's, resulting in a smaller than expected ratio of natives to plants by the late 1970's. There was no indication that survival rates for the 1970 and 1971 plants were markedly reduced from earlier years (Table 4), thus partially eliminating this explanation. The absence of a correlation between spawn-taking 'mortality' and variations in recruitment also eliminates this explanation. Because the reduced recruitment cannot be explained by changes in either survival or spawn-taking, some other explanation must be sought. The cause of this decline probably acted in 1972, because the previous decline in recruitment was anticipated from the variation in the size of the plants, survival, etc. If there were some deterioration in the substrate (D. Hughson, pers. comm.), then one would not expect such an immediate effect, unless, of course, there was a threshold effect. A host

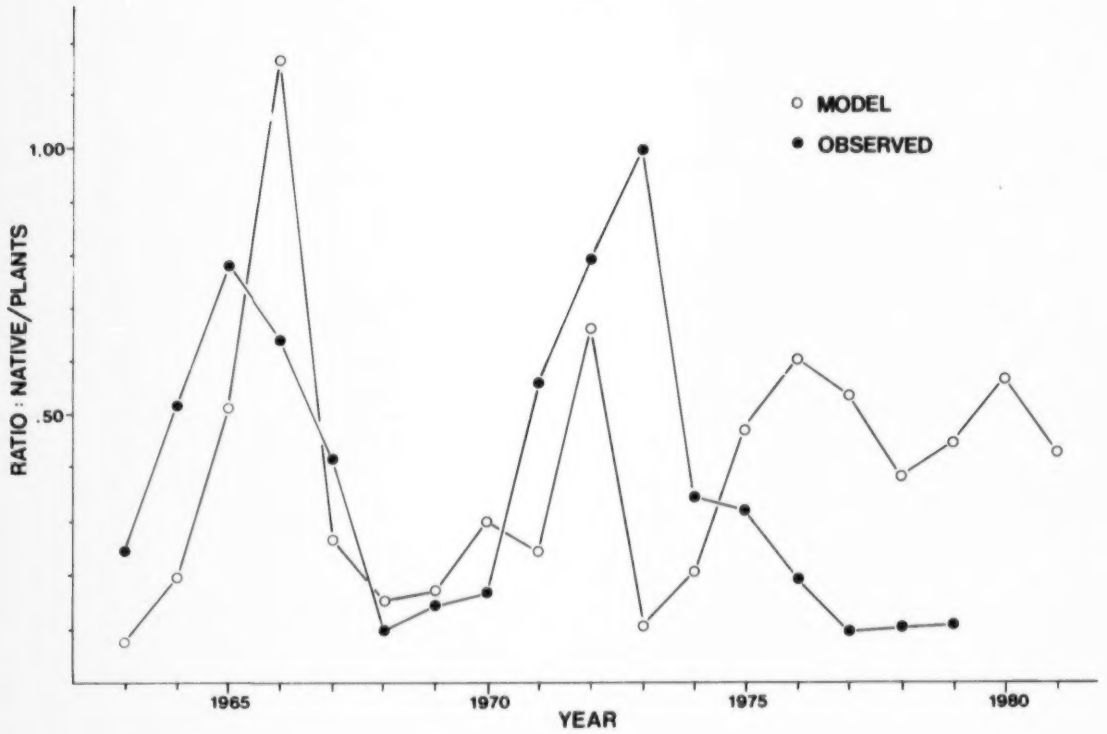

Figure 7. The observed and expected (simulation model) ratio of native to planted trout in the spawning population.

of changes could have taken place in the fauna, flora, and chemistry of the lake, but there is no evidence of this. Without more intensive work on trout, the apparent deterioration in recruitment will remain unexplained. A research programme, including the marking and recapturing of trout, will be necessary to answer these questions.

ACKNOWLEDGEMENTS

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